



# Managing biological invasions: the cost of inaction

Danish A. Ahmed<sup>1</sup> · Emma J. Hudgins<sup>2</sup> · Ross N. Cuthbert · Melina Kourantidou · Christophe Diagne · Phillip J. Haubrock · Brian Leung · Chunlong Liu · Boris Leroy · Sergei Petrovskii · Ayah Beidas · Franck Courchamp

Received: 4 March 2021 / Accepted: 10 February 2022  
© The Author(s) 2022

**Abstract** Ecological and socioeconomic impacts from biological invasions are rapidly escalating worldwide. While effective management underpins impact mitigation, such actions are often delayed, insufficient or entirely absent. Presently, management delays emanate from a lack of monetary rationale to invest at early invasion stages, which precludes effective prevention and eradication. Here, we provide such rationale by developing a conceptual model

to quantify the cost of inaction, i.e., the additional expenditure due to delayed management, under varying time delays and management efficiencies. Further, we apply the model to management and damage cost data from a relatively data-rich genus (*Aedes* mosquitoes). Our model demonstrates that rapid management interventions following invasion drastically minimise costs. We also identify key points in time that differentiate among scenarios of timely, delayed and severely delayed management intervention. Any management action during the severely delayed phase

Danish A. Ahmed, Emma J. Hudgins and Ross N. Cuthbert have contributed equally to this work.

D. A. Ahmed · A. Beidas  
Department of Mathematics and Natural Sciences, Center for Applied Mathematics and Bioinformatics (CAMB), Gulf University for Science and Technology, P.O. Box 7207, 32093 Hawally, Kuwait

E. J. Hudgins (✉) · B. Leung  
Department of Biology, McGill University, Montreal, QC H3A 1B1, Canada  
e-mail: emma.hudgins@mail.mcgill.ca

**Present Address:**  
E. J. Hudgins  
Department of Biology, Carleton University, Ottawa, ON K1S 5B6, Canada

R. N. Cuthbert  
GEOMAR Helmholtz-Zentrum für Ozeanforschung Kiel, 24105 Kiel, Germany

R. N. Cuthbert  
School of Biological Sciences, Queen's University Belfast, Belfast BT9 5DL, UK

M. Kourantidou  
Marine Policy Center, Woods Hole Oceanographic Institution, Woods Hole, MA 02543, USA

M. Kourantidou  
Institute of Marine Biological Resources and Inland Waters, Hellenic Center for Marine Research, 164 52, Athens, Greece

M. Kourantidou  
Department of Sociology, Environmental and Business Economics, University of Southern Denmark, 6705 Esbjerg, Denmark

C. Diagne · C. Liu · F. Courchamp  
Université Paris-Saclay, CNRS, AgroParisTech, Ecologie Systématique Evolution, 91405 Orsay, France

P. J. Haubrock  
Department of River Ecology and Conservation, Senckenberg Research Institute and Natural History Museum Frankfurt, Gelnhausen, Germany

results in substantial losses (> 50% of the potential maximum loss). For *Aedes* spp., we estimate that the existing management delay of 55 years led to an additional total cost of approximately \$ 4.57 billion (14% of the maximum cost), compared to a scenario with management action only seven years prior (< 1% of the maximum cost). Moreover, we estimate that in the absence of management action, long-term losses would have accumulated to US\$ 32.31 billion, or more than seven times the observed inaction cost. These results highlight the need for more timely management of invasive alien species—either pre-invasion, or as soon as possible after detection—by demonstrating how early investments rapidly reduce long-term economic impacts.

**Keywords** InvaCost · Invasive alien species · Logistic growth · Socioeconomic impacts · Prevention and biosecurity · Long-term management

## Introduction

Invasive alien species (IAS) can have deleterious impacts on ecosystem structure and function (e.g., Ricciardi and MacIsaac 2011; Bellard et al. 2017; Shabani et al. 2020), and on multiple sectors of the economy such as agriculture, fisheries and forestry (Holmes et al. 2009; Paini et al. 2016; Haubrock et al. 2021), human health (Shepard et al. 2011; Schaffner et al. 2020) and human and social well-being (Pejchar and Mooney 2009; Jones 2017). Even though many of these impacts are not yet fully understood or

quantified (Vilà et al. 2010; Kumschick et al. 2015; Crystal-Ornelas and Lockwood 2020), the scientific consensus is that IAS impacts—although variable in their nature—are massive, growing, and constitute a major driver of biodiversity loss and global change (Simberloff et al. 2013; Seebens et al. 2017; IPBES 2019; Pyšek et al. 2020). As a result, resource management agencies and conservation practitioners worldwide are continuously working to develop management tools to respond to new invasions through the prevention of introduction, limitation of spread, and mitigation of impacts (e.g., Hoffmann and Broadhurst 2016; Jones et al. 2016).

There are, however, several aspects hindering the effective management of invasive populations (Courchamp et al. 2017). In particular, the justification of management expenditures is a challenge, as management is costly, IAS are numerous and budgets are limited. Even though it is generally assumed that early responses are cost-effective in the long-term (Leung et al. 2002; Timmins and Braithwaite 2002; Russell et al. 2015), in practice, applied management is often delayed, if implemented at all. This situation is exacerbated by the fact that the proliferation of IAS and their impacts are often delayed due to time lags (Crooks 2005; Francis et al. 2021). However, while delays to perceived impact or population detectability could provide rationale for delaying management actions, a failure to consider time lags and act early can render IAS management unnecessarily expensive (Francis et al. 2021).

P. J. Haubrock  
South Bohemian Research Center of Aquaculture  
and Biodiversity of Hydrocenoses, Faculty of Fisheries  
and Protection of Waters, University of South Bohemia  
in České Budějovice, Zátěží 728/II, 389 25 Vodňany,  
Czech Republic

B. Leung  
Bieler School of Environment, McGill University,  
Montréal, QC H3A 2E7, Canada

C. Liu  
Institute of Biology, Freie Universität Berlin, 14195 Berlin,  
Germany

C. Liu  
Leibniz Institute of Freshwater Ecology and Inland  
Fisheries (IGB), 12587 Berlin, Germany

C. Liu  
Berlin-Brandenburg Institute of Advanced Biodiversity  
Research (BBIB), 14195 Berlin, Germany

C. Liu  
Institute of Hydrobiology, Chinese Academy of Sciences,  
Wuhan 430072, China

B. Leroy  
Unité Biologie des Organismes et Ecosystèmes Aquatiques  
(BOREA, UMR 8067), Muséum national d'Histoire  
Naturelle, Sorbonne Université, Université de Caen  
Normandie, CNRS, IRD, Université des Antilles, Paris,  
France

S. Petrovskii  
School of Computing and Mathematical Sciences,  
University of Leicester, University Road,  
Leicester LE1 7RH, UK

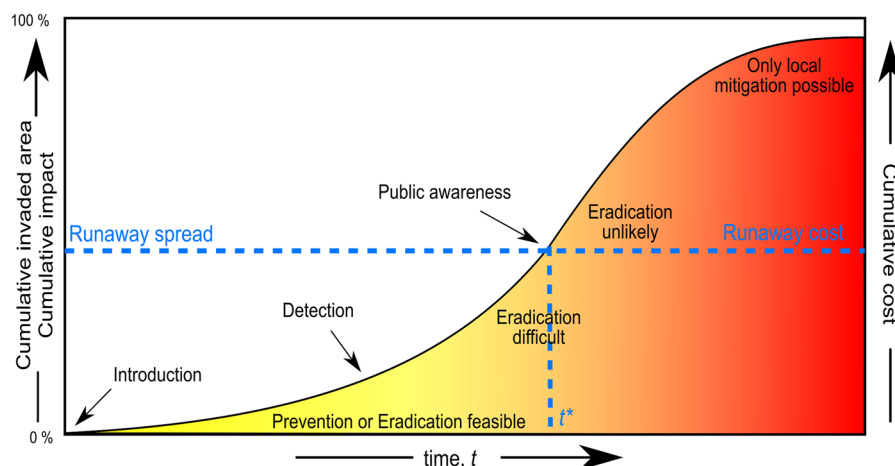
For decision makers, preventative management can be seen as a riskier strategy than waiting to control IAS after establishment, because neither its effectiveness, nor the eventual invasion of a given IAS can be predicted with high certainty (Finnoff et al. 2007). In a system where impacts are not necessarily borne by the same societal entities as those who fund management actions, immediate spending always needs to be strongly justified. In addition, with the existence of budget limitations and competing conservation needs, it is tempting to wait for impacts to be demonstrated, to be realised, or even to be severe before investing in management. In the absence of an explicit counterfactual analysis, the cost of inaction i.e., the additional expenditure due to delayed management, may be implicitly assumed to be negligible. Nevertheless, bioeconomic risk analysis, exemplified with zebra mussel invasions in US lakes, has suggested preventative measures benefit society substantially, but have been underfunded (Leung et al. 2002). Past studies have examined total invasion costs as a proxy for the benefit of prevention (Epanchin-Niell and Liebhold 2015). However, no studies have focused on a direct quantification of the monetary costs of delayed action under different invasion and management timing scenarios. Further, previous analyses have been limited to the local scale, and have relied on abundance data, which are frequently unavailable for IAS, and have used external estimates of management efficiency rather than a direct quantification (Leung et al. 2002; Hastings et al. 2006; Epanchin-Niell 2017).

For biological invasions, there thus remains a lack of justification to invest in early-stage management actions. The objective of our study is to provide a general mathematical framework for early investment from biological invasion first principles. We do this by showing that avoidable damage costs grow with management implementation delay. When management is cost-effective and does not decline in efficiency over time, delaying management leads to greater total costs (damage and management costs combined) even over very long time horizons. Even if management declines in efficiency with time, cost savings can be achieved early in an invasion by managing sooner. After a theoretical demonstration of the cost of inaction via mathematical modelling, we test our framework using empirical data for *Aedes* spp. from the InvaCost database—the most comprehensive

and up-to-date dataset of costs caused by IAS globally (Diagne et al. 2020a, b).

Our central hypothesis and model assumption is that the cumulative costs of both damage and management of IAS follow a logistic curve with time (sigmoidal-type curve). This assumption follows the well-accepted “invasion curve” (Leung et al. 2002; Lodge et al. 2016), which predicts that the area invaded or impacted by an IAS initially increases slowly, but then accelerates, and eventually reaches a plateau (Fig. 1), and is also a common pattern of growth in invasion models (Shigesada et al. 1995). If we assume that cumulative economic impact eventually saturates over time, the costs associated with a single IAS should follow a similar logistic curve. While the precise shape of the curve may depend on case-specific details (e.g., on the environmental properties or stage of invasion), the assumption of logistic IAS impacts has lacked large-scale empirical testing until recently (Ahmed et al. 2021; Cuthbert et al. 2022). Despite previous evidence for cost saturation, it is also possible that costs of an IAS may not plateau in the long term, with sustained cost increases potentially attributable to continual impacts on existing or new socioeconomic sectors coupled with ineffective long-term management. Cost saturations could additionally be an artefact of time lags in their publication and disparate reporting, and thus may differ in reality.

Given the assumption that cumulative costs are described by a logistic curve, it follows that marginal damage and management costs are distributed according to a bell-shaped curve, which decays exponentially in the long-term, eventually approaching zero. This assumption is supported by empirical cost data for several taxa (Diagne et al. 2020b), where reported costs at large timescales can be several orders of magnitude smaller than the reported maximum cost, indicating a trend towards null costs. As a result, cumulative management and damage costs saturate at their respective cost carrying capacities (see Ahmed et al. 2021). Building upon this, we formulate a theoretical cost model for marginal, realized damage costs and for the total expenditure (inclusive of damage and management costs), whilst allowing for variable management delay times and time-dependent management efficiencies. The model incorporates key parameters such as initial costs, cost growth rates and cost carrying capacities, that are useful to help better



**Fig. 1** The classical invasion curve. This relationship displays a generalized invasive alien population response over time  $t$ , after its introduction and establishment into a new environment. As the population expands and spreads, the cumulative area invaded (reported as a percentage of the total invaded area), cumulative impacts and costs (damage and management) are assumed to follow a logistic curve, thereby assuming cumulative cost saturation in the long term. There is a key point in time for management introduction at  $t = t^*$ , where

the cost of inaction is exactly half of the cost in the scenario where management is never introduced. We refer to this as a *runaway* point, where management transitions from delayed to severely delayed and thus from difficult to unlikely (see later “Cost of inaction” for a theoretical example and “Model fitting and results” for an empirical case study). Figure adapted from Invasive Plants and Animals Policy Framework, Victorian Government (2010)

understand the resulting cost dynamics. Furthermore, we compute the cost of inaction to estimate the additional expenditure due to further management delays. We demonstrate the utility of our cost model with application to the relatively data rich *Aedes* genus in the InvaCost database. In this way, we provide a coherent framework for the valuation of the foregone costs due to damages, which can be used as an imperative to manage biological invasions as proactively as possible.

## Modelling costs

Several cost-related terms are used in the following sections, and are defined in “Appendix A1” for ease of interpretation.

### Damage and management costs

In developing a theoretical cost model, we focused on reactive management, i.e., the scenario where

management is introduced after the arrival and establishment of an IAS. As a first step, following the classical invasion curve (see Fig. 1), we assumed that the cumulative damage cost as a function of time  $C(t)$  in the absence of management onset is modelled by a sigmoidal-type curve given by the (modified) logistic function:

$$C(t) = \frac{K(1 - e^{-rt})}{1 + \left(\frac{K}{A} - 1\right)e^{-rt}}, \quad C(0) = 0, \quad C(\infty) = K \quad (1)$$

where  $r$  is the intrinsic growth rate of damage costs,  $K$  is the cumulative damage cost in the long term (henceforth referred to as the damage cost carrying capacity), and  $A$  is a parameter which modulates the shape of the logistic curve.

It follows that the marginal (or instantaneous) damage cost  $D(t)$  can be computed as the derivative of Eq. (1), resulting in the logistic distribution (bell-shaped curve), given as:

$$D(t) = \frac{dC(t)}{dt} = \frac{rK \left(1 + \frac{K}{A}\right) e^{-rt}}{\left(1 + \frac{K}{A} e^{-rt}\right)^2}, \quad D(0) = D_0 = \frac{rK}{1 + \frac{K}{A}}, \quad D(\infty) = 0 \quad (2)$$

where  $D_0$  is the initial damage cost, which can be expressed solely in terms of the parameters  $r, K$  and  $A$ . It can be readily shown that the marginal damage cost reaches a maximum value of  $D_{\max} = \frac{1}{4}r(A + K)$  at time  $t = \frac{1}{r} \ln\left(\frac{K}{A}\right)$ .

With the onset of reactive management, the impact of an invasion decreases, and therefore so does the cost incurred due to damages. Since the cumulative management cost is also assumed to depend on the stage of invasion, it can also be modelled as a logistic curve, albeit with a different intrinsic growth rate  $r_M$  and management cost carrying capacity  $K_M$ . Therefore the marginal management cost  $M(t - \tau)$  delayed by  $\tau$  years is analogous to Eq. (2) (i.e., bell-shaped curve) and can be described as:

$$M(t - \tau) = \frac{r_M K_M \left(1 + \frac{K_M}{A_M}\right) e^{-r_M(t-\tau)}}{\left(1 + \frac{K_M}{A_M} e^{-r_M(t-\tau)}\right)^2} \times H(t - \tau), \quad M(0) = M_0 = \frac{1}{2} \times \frac{r_M K_M}{1 + \frac{K_M}{A_M}}, \quad M(\infty) = 0 \quad (3)$$

where  $H(t - \tau)$  is a unit step function with value 0 if  $t < \tau$ ,  $\frac{1}{2}$  if  $t = \tau$  and 1 if  $t > \tau$  and  $M_0$  is the initial management cost. The maximum marginal management cost is  $M_{\max} = \frac{1}{4}r_M(A_M + K_M)$  and occurs at time  $t = \frac{1}{r_M} \ln\left(\frac{K_M}{A_M}\right) + \tau$ . Note that when  $\tau = 0$ , Eq. (3) corresponds to a scenario with immediate management action. In general, it is expected that  $M_0, M_{\max}$  and  $K_M$  are much smaller than  $D_0, D_{\max}$  and  $K$ , respectively, as supported by invasion cost data at the global scale (Cuthbert et al. 2022; Diagne et al. 2021).

We assume that the management expenditure directly reduces the cost due to damages, and therefore once management is introduced at time  $t = \tau$ , the realized marginal damage cost  $D^*$  is:

$$D^*(t, \tau) = D(t) - E(t - \tau) \times M(t - \tau) \quad (4)$$

which is a positive quantity, or otherwise equal to zero. Within this equation, we propose a management efficiency term  $E$  as a function of time:

$$E(t - \tau) = 1 + \frac{(E_0 - 1)(E_1 - 1)}{(E_0 - 1) + (E_1 - E_0)e^{-\alpha(t-\tau)}}, \quad 0 < E_0 < E_1 \quad (5)$$

where  $E_0$  is the initial efficiency value when management is introduced at time  $t = \tau$ ,  $\alpha$  is the efficiency growth rate, and  $E_1$  serves as a maximum efficiency value in the case  $\alpha > 0$ , or otherwise regulates the shape of the efficiency curve. The efficiency function  $E$  quantifies the amount of reduction in the damage cost for every \$ 1 spent on management over time.

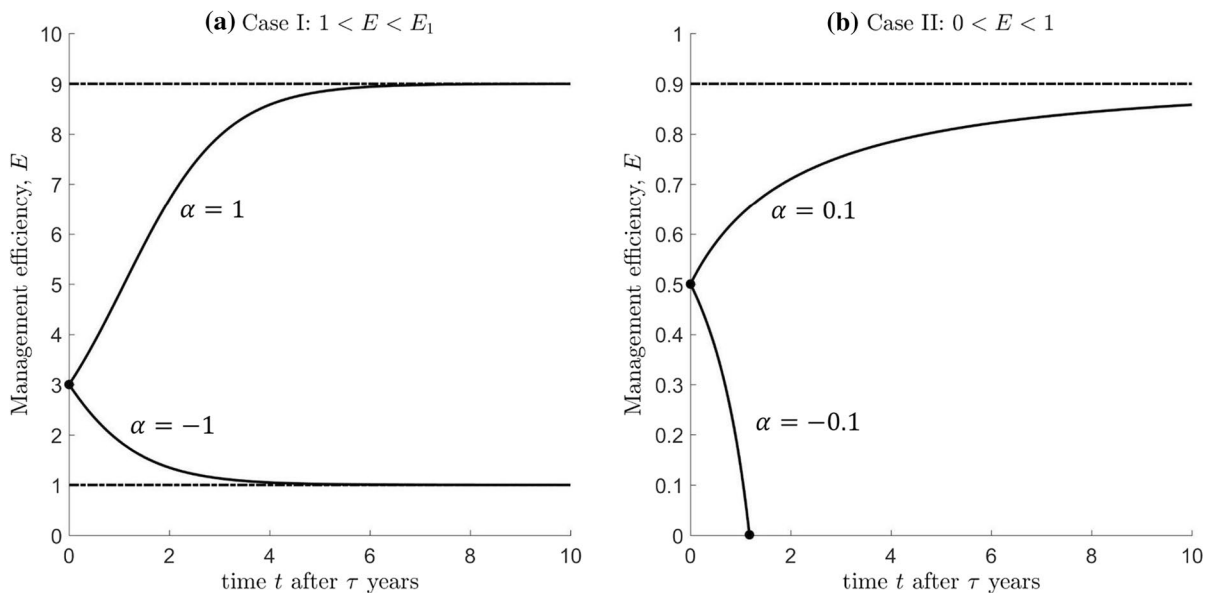
With management action, the total cost  $T$  incurred by the invasion is the sum of realized damage and management costs:

$$T(t, \tau) = D^*(t, \tau) + M(t - \tau). \quad (6)$$

We deem management to be 'effective' only if the total cost is less than the potential cost due to damages i.e.,  $T < D$ , which occurs if damage costs decrease by an amount greater than \$ 1 for every \$ 1 spent on management, and is otherwise considered ineffective.

The behaviour of the management efficiency function  $E$  is as follows:

- I. If  $E$  lies between 1 and  $E_1$  for all time, then management is effective. Starting from an initial value of  $E_0$ , management efficiency can either increase, decrease or remain constant depending on the growth rate  $\alpha$ . If  $\alpha > 0$ , the efficiency grows approaching a maximum value of  $E_1$  in the long term, whereas if  $\alpha < 0$ , the efficiency decays to 1, and if  $\alpha = 0$ , the efficiency remains constant at  $E_0$  (see Fig. 2a).
- II. If  $E$  lies between 0 and 1 for all time, then management is not only ineffective, but also counterproductive, as \$ 1 spent on management reduces the damage cost by less than \$ 1, and



**Fig. 2** Management efficiency function  $E$  given by Eq. (5). Efficiency parameters for **a** Case I are  $E_0 = 3$ ,  $E_1 = 9$ ,  $\alpha = 1$  or  $-1$ , and for **b** Case II  $E_0 = 0.5$ ,  $E_1 = 0.9$ ,  $\alpha = 0.1$  or  $-0.1$ . Parameter values are chosen for illustrative purposes

thus the total cost exceeds that of potential damages, i.e.,  $T > D$ . In this case,  $E_0$ ,  $E_1$  and  $\alpha$  play a similar role to that described in (I), except that in the case  $\alpha < 0$  the efficiency decreases rapidly to zero (see Fig. 2b).

In the special case that  $E$  is equal to 1 for all time (which occurs if either  $E_0$  or  $E_1$  are equal to 1), then management is ineffective as \$ 1 spent on management reduces the damage cost by \$ 1, and thus the total cost is exactly the same amount as that of potential damage, i.e.,  $T = D$ .

Figure 3 illustrates the behaviour of the cost model described by Eqs. (2)–(6) for the damage cost  $D$ , management cost  $M$ , realized damage cost  $D^*$  and the total cost  $T$ . For illustrative purposes, we consider scenarios with effective management ( $E_0 = 2 > 1$ ) with increasing efficiency ( $\alpha = 0.01 > 0$ ) or decreasing efficiency ( $\alpha = -0.01 < 0$ ), with either immediate ( $\tau = 0$ ) or delayed ( $\tau = 20 > 0$ ) management action. Note that since management is deemed to be effective, both  $D^*$  and  $T$  are less than  $D$  once management is introduced.

The cost dynamics differ depending on whether management efficiency increases or decreases over

time. In the case of increasing efficiency ( $\alpha > 0$ ) the maximum costs for  $D^*$  and  $T$  are lower than in the case of decreasing efficiency ( $\alpha < 0$ ), and these maxima occur earlier if management is delayed (Table 1). Also, irrespective of  $\alpha$ ,  $D^*$  and  $T$  approach zero faster in the presence of a management delay compared to immediate management, c.f. Figure 3 plots (c and d). However, note that both  $D^*$  and  $T$  exhibit larger maximum cost values with delayed management (Table 1).

#### Cost of inaction

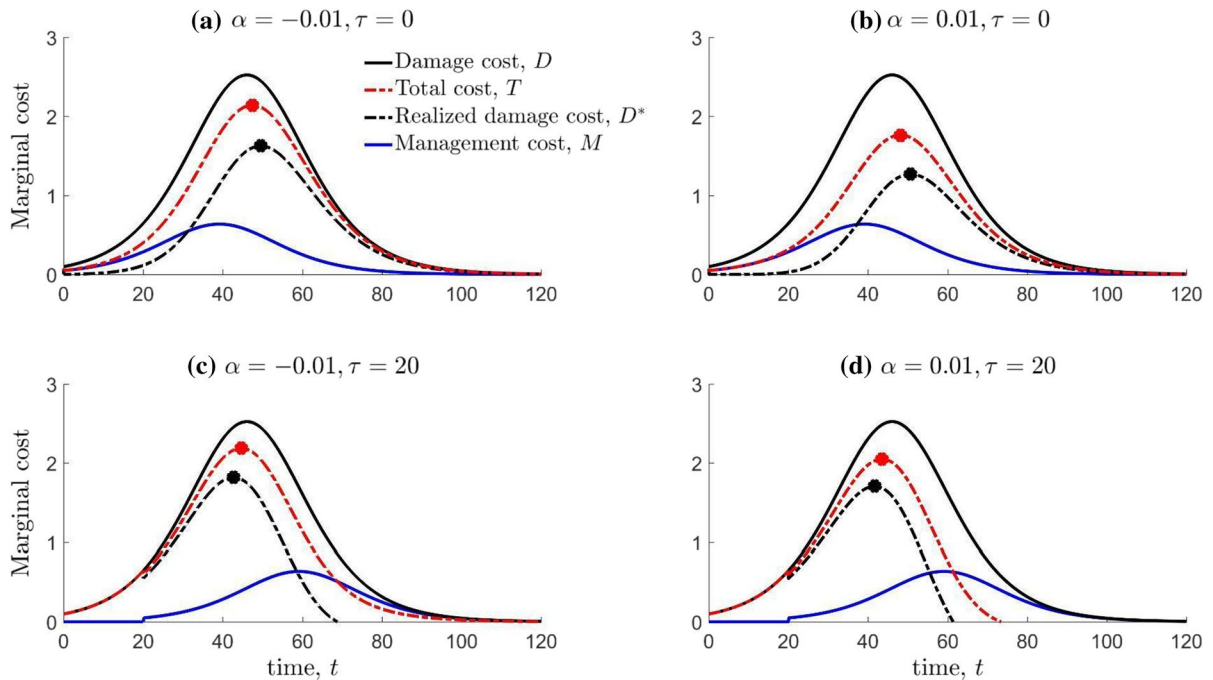
We define the marginal cost of inaction  $\varphi$  as the cost difference at time  $t$  between two distinct scenarios where management is introduced at a fixed time  $\tau^*$  and at a further delayed time  $\tau$ , given as:

$$\varphi(t, \tau) = T(t, \tau) - T(t, \tau^*), \quad \tau > \tau^* \quad (7)$$

which is a positive quantity, or otherwise equal to zero. The cumulative cost of inaction  $\Phi$  is then given by:

$$\Phi(t, \tau) = \int_0^t [T(t', \tau) - T(t', \tau^*)] dt' \quad (8)$$





**Fig. 3** Cost model behaviour over time for selected parameters:  $r = 0.1$ ,  $K = 100$ ,  $A = 1$ ,  $D_0 = 0.099$ ,  $r_M = 0.1$ ,  $K_M = 25$ ,  $A_M = 0.5$ ,  $M_0 = 0.026$ ,  $E_0 = 2$ ,  $E_1 = 5$ , illustrated at four sets of values of  $\alpha$  and  $\tau$  across panels **a–d**. Initial costs  $D_0, M_0$  are computed from  $A, A_M$ , respectively, see Eqs. (2) and (3). We consider scenarios of decreasing or increasing efficiency, with

immediate or delayed management. The maximum costs for  $D^*$  and  $T$  are indicated with black/red markers with values listed in Table 1. Note that the bell-shaped curve for marginal costs shown here results in logistic (sigmoidal) growth of cumulative costs (see also “Damage and management costs”)

**Table 1** Time of occurrence and maximum cost values for the realized marginal damage cost  $D^*$  and the total cost  $T$ , as indicated in Fig. 3

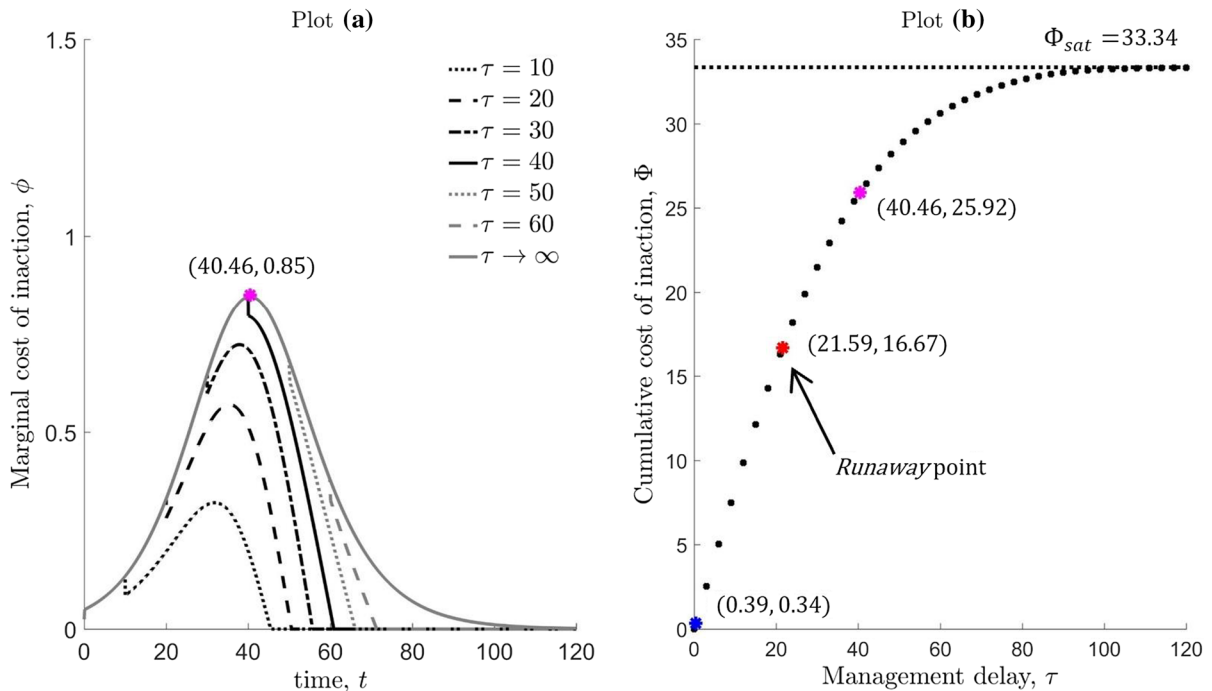
$D^*$	$\alpha = -0.01$	$\alpha = 0.01$	$T$	$\alpha = -0.01$	$\alpha = 0.01$
$\tau = 0$	(49.53, 1.63)	(50.68, 1.27)	$\tau = 0$	(47.46, 2.14)	(48.17, 1.76)
$\tau = 20$	(42.70, 1.82)	(41.67, 1.71)	$\tau = 20$	(44.65, 2.19)	(43.51, 2.05)

which is the total additional expenditure at time  $t$  due to delayed management intervention. The integral in Eq. (8) is not analytically tractable, however an approximation can be determined using techniques of numerical integration (i.e., trapezoidal rule).

Figure 4a shows that with no management intervention ( $\tau \rightarrow \infty$ ), the marginal cost of inaction increases rapidly, reaching a peak at time 40.46 with cost value 0.85, and then subsequently decays to zero in the long-term. This peak serves as a critical point where inaction costs transition from increasing to decreasing. With the introduction of management, the marginal cost of inaction  $\varphi$  ‘dips’ due to the direct

impact of the initial management on damage costs. Following this, the cost dynamics depend on the delay time  $\tau$  relative to when the critical point occurs. If  $\tau < 40.46$ ,  $\varphi$  continues to grow even after management onset, eventually reaching a peak with subsequent decay until the cost of inaction is zero. Note that the maximum inaction cost (peak) is lower with earlier management. In contrast, if  $\tau \geq 40.46$ , then  $\varphi$  decreases monotonically to zero cost. In general,  $\varphi$  is lower and approaches zero much quicker with earlier management intervention.

Figure 4b shows that the cumulative cost of inaction  $\Phi$  increases rapidly with management delay



**Fig. 4** **a** The marginal cost of inaction  $\phi$ , defined as the difference in total costs between scenarios with management delay  $\tau$  (varied) and immediate management action  $\tau^* = 0$ , see Eq. (7). The maximum value for  $\phi$  remains at 0.85 if the delay time  $\tau$  exceeds 40.46, but can be lower at earlier times. **b** The cumulative cost of inaction  $\Phi$  evaluated retrospectively (in the long-term  $t \rightarrow \infty$ ), whilst considering different management delay times  $\tau$  relative to immediate management action  $\tau^* = 0$ , see

Eq. (8). The coloured markers represent points that differentiate among scenarios of the severity of delayed management. In the long term, the additional expenditure in the absence of management is estimated at  $\Phi_{sat} = 33.34$ . All parameter values are the same as that in the caption of Fig. 3, except that we only consider the case where management efficiency is increasing with time,  $\alpha = 0.01 > 0$ , see also Fig. 3 plots (b) and (d)

$\tau$ , eventually approaching a saturation level that represents a potential additional expenditure of  $\Phi_{sat} = 33.34$  in the absence of management intervention ( $\tau \rightarrow \infty$ ). We identify three key markers along  $\Phi$  which represent time windows that can inform management decisions. First, the blue marker represents 1% of  $\Phi_{sat}$ , occurring at  $\tau = 0.39$  with  $\Phi = 0.34$ . The 1% threshold was chosen to indicate a period when small losses have been incurred compared to the potential cost of never managing. Second, the red marker is a runaway point which represents 50% of  $\Phi_{sat}$ , occurring at  $\tau = 21.59$  with  $\Phi = 16.67$ . Last, the magenta marker is the critical point where the marginal cost of inaction peaks as shown in Fig. 4a,

occurring at  $\tau = 40.46$  with  $\Phi = 25.92$  (amounting to approx. 77% of  $\Phi_{sat}$ ).

In this illustrative example (Fig. 4b), we can consider management intervention to be timely if  $\tau < 0.39$ , delayed if  $0.39 < \tau < 21.59$ , severely delayed if  $21.59 < \tau < 40.46$ , and propose that only small-scale local management is feasible if  $\tau > 40.46$ . These time windows can be interpreted analogously to the different phases in the classical invasion curve presented in Fig. 1, where managing the invasion transitions from feasible, to difficult, to unlikely, to nearly impossible with increasing management delay.



## Empirical case study for *Aedes* spp

### InvaCost database

At the time of analysis (August 2021), the InvaCost database (version 4.0) included 13,123 cost entries (i.e., rows of cost data reported for a particular species in a particular location to a particular economic activity sector) from systematic and opportunistic literature searches conducted primarily in English, and altogether in 15 languages (Diagne et al. 2020b; Angulo et al. 2021). This database captures reported economic costs associated with IAS in their non-native range (incurring costs from management, damage and losses). Notably, cost reporting is unevenly distributed geographically, taxonomically and temporally in InvaCost (Diagne et al. 2021), but this is largely due to underlying biases in IAS research rather than the database itself (Pyšek et al. 2008). Data were obtained through systematic literature searches conducted on the Web of Science, Google Scholar and Google search engine (Diagne et al. 2020b), as well as opportunistic contacting of relevant experts to augment these data. InvaCost is a dynamic database that is expected to continue growing as more cost information becomes available in future. The version used for this study includes 1200 unique species or species combinations and 1872 documents reporting costs. A full description of the data sources, cost search protocols and spatial coverage is available in Diagne et al. (2020b).

The data in InvaCost are recorded with several descriptors (over 60 in InvaCost version 4.0, see <https://doi.org/10.6084/m9.figshare.12668570> for complete details) and standardised against a single currency (2017 US\$). This currency was selected as it is a common metric in environmental economics, standardised to 2017 to account for inflation in the year of the main cost search. These descriptors include, among other things, the cost type (“Type of cost merged”), which groups costs into three distinct categories: (a) “Damage” referring to damages or losses incurred by the invasion (e.g., costs for damage repair, resource losses, medical care), (b) “Management” comprising any expenditures dedicated to prevent, limit and/or mitigate invasion impacts (e.g., monitoring, prevention, control, education, eradication) and (c) “Mixed” including indistinguishable damage and management costs (cases where reported

costs were not clearly separable from the aforementioned cost types categories). We considered all types of damage costs, but only post-invasion management costs, in order to eliminate preventative management (i.e., for species that have not yet arrived). This was done using the “Management\_type” column of the database by selecting the “Post-invasion management” category therein. We further filtered our dataset to examine only costs incurred at larger scales (up to national), using only “Country” and “Site” spatial scales from the “Spatial\_scale” column. We also removed any extrapolated (“Potential”) costs (i.e., those extrapolated from different spatial scales) by limiting our search to “Observed” costs in the “Implementation” column. Furthermore, we considered only costs in peer-reviewed literature and official documents, or grey literature with fully reproducible methods, defined as having “High” reliability under the “Method\_reliability” column (Diagne et al. 2020b).

For consistency and to aid comparisons across data, all costs in the original database were ‘expanded’ so that cost entries could be considered on an annual basis. This means that single cost entries spanning multiple years (e.g., \$ 10 million between 2001 and 2010) were divided into distinct entries according to their duration (e.g., \$ 1 million for each year between 2001 and 2010, corresponding to ten entries in the expanded database). Expansion was done using the *expandYearlyCosts* function of the ‘invaCost’ R package (Leroy et al. 2020), which repeats the annual cost for each database entry according to the estimated time range of impacts provided with each reference in the InvaCost database (but see “Description of the *Aedes* spp. data” for a reweighting done in the case of 70 years of constant costs). For the purposes of our model, each datapoint refers to a single year of cost data aggregated across InvaCost entries globally for a given genus.

### Description of the *Aedes* spp. data

In order to test our theoretical cost model, we present the case study of *Aedes* spp. (see later “Model fitting and results”). This genus was chosen as it is the richest in data, with both damage and management costs reported continuously on an annual basis over long-time periods. The costs (extracted from the InvaCost database version 4.0) corresponded to 232 individual publications, which, when expanded, corresponded

to 819 entries spanning years 1921 ( $t = 0$ ) to 2016 ( $t = 95$ ). Damage costs spanned the entire time period, amounting to 134 publications and 631 expanded entries. Damage cost values ranged from  $\$ 9.49 \times 10^{-6}$  billion to  $\$ 0.24$  billion for the first and last years, respectively, with a maximum reported cost of  $\$ 4.61$  billion in 2006 ( $t = 85$ ).

Since the *expandYearlyCosts* function was used for the *Aedes* spp. data, it led to costs from single publications reported over long time periods being re-distributed evenly. As a result, 70 out of the 74 reported damage costs in the first 73 years were repeated, with a total sum amounting to  $\$ 0.23$  billion. Although this expansion function provides a simple means to re-distribute costs, it is unrealistic with regards to the likely dynamics of economic impacts over this long-time horizon and was chosen as a basic representation by the ‘invacost’ package developers. As a more plausible alternative, we chose to re-distribute the first 73 years of costs as a geometric series, whilst ensuring that the total costs summed to the same value over that time period. This assumes that costs continue to increase annually, as can be expected during the early phase of an invasion (see [github.com/emmajhudson/CostOfInaction](https://github.com/emmajhudson/CostOfInaction) for code and transformed data).

Management costs corresponded to 98 publications, which produced 188 expanded entries. Management was introduced in 1976 ( $t = 55$ ) with cost  $\$ 0.02$  billion and occurred until 2017 ( $t = 96$ ) with value  $\$ 1.43 \times 10^{-3}$  billion. To avoid undue influence of high leverage costs, we removed two extreme cost records within the management data that exceeded 1.5 interquartile ranges above the third quartile: a cost of  $\$ 1.19$  billion in 2012 ( $t = 91$ ) and one of  $\$ 0.67$  billion in 2016 ( $t = 95$ ). Once these outliers were removed, the maximum management cost was  $\$ 0.22$  billion, reported in 2001 ( $t = 80$ ).

## Model fitting and results

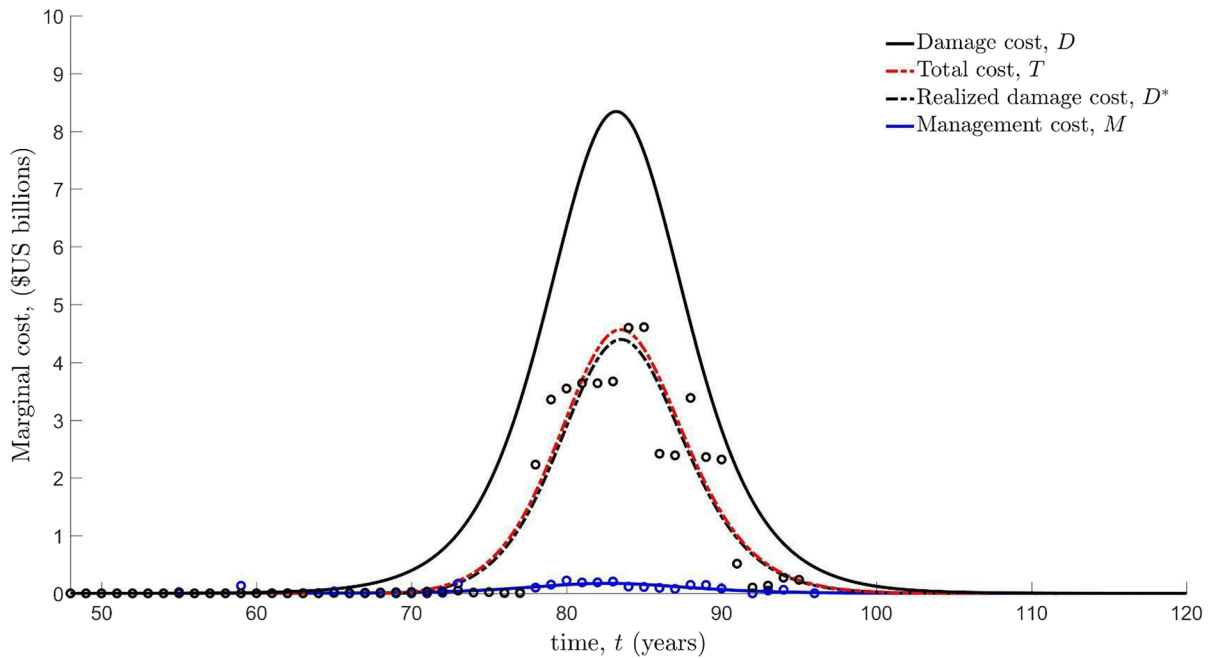
The cost model described by Eqs. (2)–(5) was tested against the *Aedes* spp. cost data. The least-squares non-linear regression curve fitting tool *lsqcurvefit* from Matlab was used to find the best-fitting curves for management costs  $M$  and realized damage costs  $D^*$ , by minimising the sum of the squares of the residuals (i.e., difference between the cost data points and the fitted values provided by the cost curves). A management delay time of  $\tau = 55$  years was used in the

computation, which corresponds to the first reported management cost in the year 1976. The curve fitting tool provided estimates of the model parameters for management costs  $r_M, K_M, A_M$ , management efficiency  $E_0, E_1, \alpha$ , and realized damage costs  $r, K, A$ . The initial costs at the time of first detection  $M_0, D_0$  were then computed from  $A_M$  and  $A$ , respectively, using Eqs. (2) and (3). See “Appendix A2” for definitions of these cost parameters. Once model parameters were estimated, the potential damage cost  $D$  in the absence of management and the total cost  $T$  were determined from Eqs. (2) and (6). The strengths of the curve fittings were quantified by the coefficient of determination  $R^2$  and the root mean squared error *RMSE*.

Figure 5 illustrates that the theoretical cost model was highly predictive of the marginal management and damage cost data for *Aedes* spp.,  $R^2 = 0.57$  and  $0.91$ , respectively. We estimated that with a management delay of 55 years, the maximum management expenditure amounted to  $\$ 0.17$  billion, resulting in a significant reduction of the maximum damage cost from  $\$ 8.34$  billion to  $\$ 4.39$  billion ( $\sim 47\%$  decrease), and a total maximum cost of  $\$ 4.56$  billion.

Figure 6 shows the cumulative cost of inaction  $\Phi$  which determines the additional expenditure due to delayed management relative to the scenario where management is introduced in 1969 ( $\tau^* = 48$ ). We found that  $\Phi$  remained very low for a short time period, with a subsequent rapid increase, and eventually approached saturation i.e., the estimated no action cost  $\Phi_{sat} = \$ 32.31$  billion. The base year of 1969 was chosen since it is the first instance where the reported damage cost (of value  $\$ 0.12$  million) exceeds the estimated initial management cost  $M_0 = \$ 0.11$  million. Moreover, the sum of all reported costs over the time period  $t < 48$  is  $\$ 0.42$  million, amounting to  $< 0.01\%$  of  $\Phi_{sat}$ , and thus provides a negligible contribution. To put the magnitude of these estimated costs into perspective, note that the long-term cumulative cost of damages in the absence of management amounts to approx.  $K = \$ 100$  billion.

We identified four markers of relevance in Fig. 6. First, the blue marker represents a cumulative cost value  $\$ 0.32$  billion when management is introduced at  $\tau = 52.63$  years after the first recorded damage cost, which is 1% of the expenditure in the scenario where no action is ever taken, i.e.,  $\Phi_{sat}$ . Second, the red marker (*runaway* point) occurs at delay time



**Fig. 5** Best-fitted curves for management costs  $M$  and realized damage costs  $D^*$  with a delay time of  $\tau = 55$ . Estimated model parameters for management costs  $r_M = 0.29$ ,  $K_M = 2378$ ,  $A_M = 0.77$ , management efficiency  $E_0 = 1.44$ ,  $E_1 = 23.09$ ,  $\alpha = 0.65$ , realized damage costs  $r = 0.33$ ,  $K = 100000$ ,  $A = 0.79$ , and initial costs  $M_0 = 0.11$ ,  $D_0 = 0.26$  computed from  $A_M$  and  $A$ , respectively. See “Appendix A2” for a description of parameters, their units and their estimated values to

a higher degree of accuracy. Strength of curve fitting metrics  $R^2 = 0.57$ ,  $RMSE = \$48.35$  for management costs and  $R^2 = 0.91$ ,  $RMSE = \$453.83$  for realized damage costs. Note that the parameters that relate to the magnitude of costs are in US\$ millions, whereas the figure is re-scaled to \$ billions for illustrative purposes. Given these parameter estimations, the potential damage costs  $D$  and the total cost  $T$  were determined from Eqs. (2) and (6)

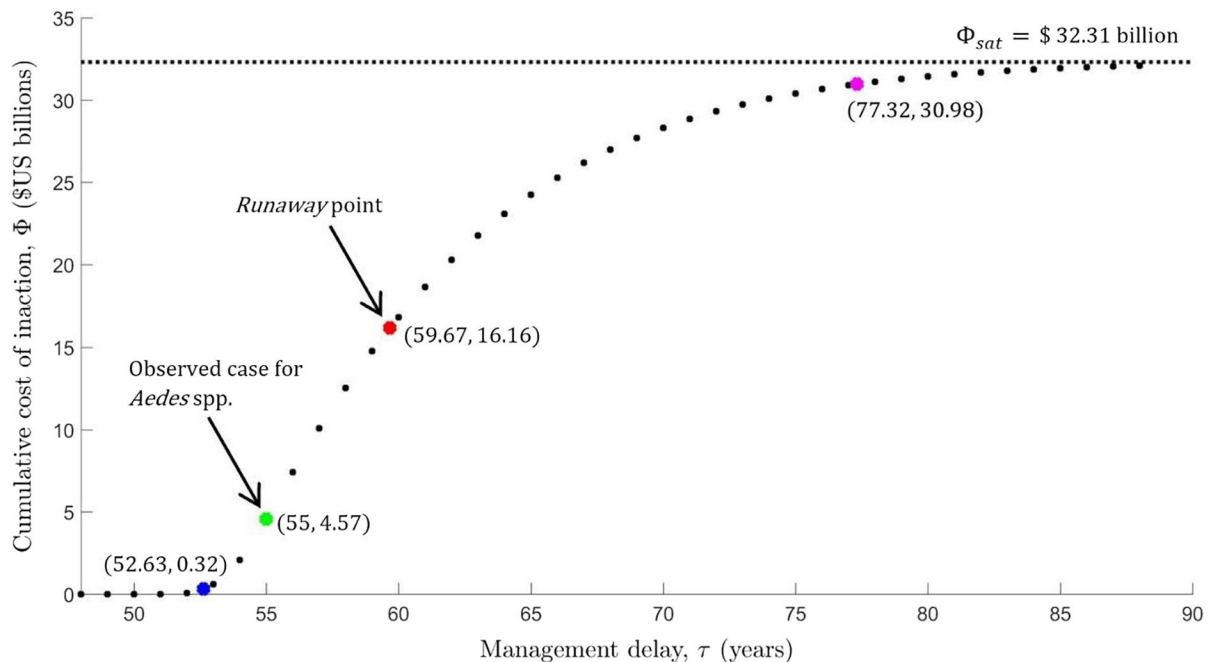
$\tau = 59.67$  years, where  $\Phi$  amounts to \$ 16.16 billion, which is approx. 50% of  $\Phi_{sat}$ . Management intervention prior to this point would lead to < 50% of the amount of losses incurred in comparison to a no action scenario. Third, the magenta marker (critical point where the marginal cost of inaction peaks) occurs at  $\tau = 77.32$  years with  $\Phi = \$30.98$  billion (approx. 96% of  $\Phi_{sat}$ ), indicative of severely delayed management with little prospect of cost savings. Last, the green marker represents the currently observed scenario within InvaCost considering *Aedes* spp. ( $\tau = 55$  years), with estimated total losses amounting to \$ 4.57 billion (14% of  $\Phi_{sat}$ ); a considerable amount that could have been saved with earlier management intervention.

In general, any management intervention during the period between the blue and red markers can be considered ‘delayed’, with cost impacts of delay exacerbated closer to the latter marker. However, this allows us to identify a short time window

of opportunity from 52.63 to 59.67 years ( $\sim 7$  years) for potential large savings, precisely during a phase where  $\Phi$  increases rapidly. Note that the observed scenario for *Aedes* spp. lies within this timeframe, suggesting delayed management, albeit with losses only amounting to approximately 14% of the potential no action cost,  $\Phi_{sat}$ . Beyond the runaway point, management can be considered ‘severely delayed’ with losses approaching  $\Phi_{sat}$ .

## Discussion

Our work highlights that failing to begin managing an invasion can quickly lead to immense economic costs. The cost of inaction increases rapidly prior to a certain threshold time, after which the rate of accumulation slows down, and eventually saturates at a high level (see Fig. 6). This means not only that IAS costs can quickly increase to unbearable amounts, but also



**Fig. 6** The cumulative cost of inaction  $\Phi$  for *Aedes* spp. computed retrospectively (in the long-term  $t \rightarrow \infty$ ) for different management delay times  $\tau$ , relative to  $\tau^* = 48$ , using Eq. (8). Coloured markers represent points that differentiate among scenarios of the severity of delayed management. In the long-

term, the additional expenditure in the absence of management is estimated at  $\Phi_{sat} = \$ 32.31$  billion. All estimated parameter values are mentioned in the caption of Fig. 5, see also “Appendix A2”

that they may initially be deceitfully slow to accrue, therefore not signalling to policy makers the urgency to invest in management. Indeed, during this initial time period, the willingness to allocate funds to IAS management may be low due to the lack of perceived risk or impact detection (Finnoff et al. 2007). A lack of willingness to invest may also represent a potential moral problem, whereby invader impacts are seemingly incurred by other regions, sectors, or generations than those that take management action—paralleling challenges in moral responsibilities for climate change (Gardiner 2006). However, as we have shown here, these costs can inflate suddenly and potentially overwhelm major sectors of the economy.

Our findings are generally in line with the resource economics literature and associated bioeconomic analyses that suggest a higher value for today’s benefits compared to future benefits, owing to the discounting principle (Clark 1990). This is because today’s benefits can be invested and yield more value through time, which confers a higher advantage compared to delaying those benefits. This in turn implies

that the effect of control actions applied earlier are worth more, which also explains why prevention and early action are also prominent in bioeconomic analyses for invasions (Hui and Richardson 2017; see also McDermott et al. 2013; Polasky 2020 for more examples of how early identification and removal bears the strongest benefits). These findings tie into efforts to combat policy makers’ hesitancy to commit to more proactive management spending, given limited conservation budgets that could alternatively be used only for reactive management actions. Bioeconomic frameworks using real options theory have shown that, particularly in cases of fast-spreading species where expansion is too fast and unpredictable, immediate action is the only option (Sims et al. 2016). Controlling such species immediately has large potential returns and therefore incentivizes larger investments, even if the spread’s volatility increases the risk in these investments (Sims et al. 2016).

Since our theoretical cost model predicts the damage cost and total expenditure from model fitting against realized damage and management cost data

(see Fig. 5), it provides a simpler yet conceptual description of the resulting cost dynamics, in contrast to more complex models that are reliant on time series of IAS abundances (Leung et al. 2002). Also, our approach goes beyond prescriptive frameworks for optimal control, as it allows for a direct estimation of management efficiency from empirical cost data. Further, our approach is focused at the global rather than regional or site-specific scales. As such, we show that when management is effective ( $E > 1$ ) and less costly than damage: (i) initiating management at any time can reduce the total cost of a given IAS over a short time period; (ii) greater reductions in the total expenditure are achieved with increasing management efficiency (see Table 1, Fig. 3); and (iii) there are critical time windows that distinguish among timely, delayed and severely delayed management, corresponding to different phases of the invasion curve, where IAS eradication transitions from feasible to difficult and to unlikely, respectively (see Fig. 1). Importantly, (iv) we compute the time taken to reach the *runaway* point, where initiation of management action prior can lead to a considerable amount of cost savings ( $< 50\%$  of the potential cost in the absence of management), with more cost savings given earlier management (see Fig. 6). Also, note that the model also allows not only for an estimation of the cost of inaction but also of the reverse scenario, i.e., estimating the cost savings of timely management based on counterfactual analyses of hypothetical delays.

In the *Aedes* case study, the cost of inaction grew relatively slowly over an initial 53 year period, but then accumulated rapidly within a critical ~seven year period by at least two orders of magnitude. This resulted from a sudden rapid increase in the cost due to damages, combined with a delayed suboptimal management strategy (see Fig. 6). In practice, this window of opportunity may be difficult to identify due to context-dependencies that influence invasion debt as well as the magnitude of impact and differences in detection timing among regions. These challenges indicate that acting sooner, even when costs accrue slowly, is the optimal risk averse strategy (see also Leung et al. 2002). Given these uncertainties, we suggest that policy makers should prioritise investments at the earliest possible invasion stage to improve efficiency and reduce future invasion costs, while also maintaining effort to curtail the invasion

and increasing awareness of IAS impacts throughout the duration of the invasion. Additionally, the fact that the cost of inaction saturates in the long-term should not deter management effort at late invasion stages, whereby control can still be effective and help mitigate ongoing and emerging ecological and socio-economic impacts through, for example, novel arbovirus emergence in our *Aedes* model taxon (Barrera et al. 2019). Indeed, despite management being delayed by 55 years and incurring an inaction cost of \$ 4.57 billion (14% of the maximum), our model estimates that an additional cost of \$ 27.74 billion (86%) could have been incurred in the absence of any *Aedes* management whatsoever. As a cautionary note, given that we only presented a single case study for *Aedes* spp., the model should be treated as a conceptual one, and our aim is not to be prescriptive about the costs of inaction. Rather, this should be seen as an illustrative example, where cost estimates are subject to improvements upon availability of more refined data, and further development of the underlying model with added complexity to better reflect reality. This point may be particularly pertinent for management costs, given the relatively low  $R^2$  for marginal management cost data (0.57) compared to marginal damage cost data (0.91). For management spending, greater variability may be exhibited because management is a decisive action that is influenced by wider social, political and economic contexts that vary through time.

In the cost model, damage and management costs are parametrized by their initial costs ( $D_0$ ,  $M_0$ ), intrinsic cost growth rates ( $r$ ,  $r_M$ ) and cost carrying capacities ( $K$ ,  $K_M$ ), as per “Appendix A2”. Although we demonstrated an example with *Aedes*, the model can be applied to other genera, and parameters can thus be estimated given the availability of sufficient empirical cost data for these taxa. We expect these parameters to be inherently affected by, for example, the taxonomic group, size of the invadable area, introduction pathways and traits of IAS. In light of this, we predict that large-bodied IAS such as raccoons and squirrels (*Procyon*, *Callosciurus*), as well as other rapidly spreading invaders, such as ballast water/hull contaminants (e.g., mollusks and copepods; Lin et al. 2020) may have high cost growth rates  $r$ . In contrast, genera similar to *Aedes* that may not necessarily disperse rapidly at continental scales, but have potential for triggering significant costs, could exhibit high cost carrying capacities  $K$  in spite of lower cost growth rates. IAS with both a large capacity for damage



and a fast growth in costs would have high  $r$  and  $K$  values. These patterns would likely be similar for the fall armyworm (*Spodoptera frugiperda*), which has spread rapidly throughout Africa and Asia with high economic impacts on agriculture (Abrahams et al. 2017). Other species we suspect will show this pattern are the Asian hornet *Vespa velutina* and the lionfish *Pterois volitans*, as they are among the fastest spreading IAS in terrestrial and marine realms, respectively, and are also known to have very high management and/or damage impacts (Barbet-Massin et al. 2020; Diagne et al. 2020a).

While our base model assumption is that cumulative costs follow a logistic curve (sigmoidal-type), from which we derive that marginal costs are logistically distributed (bell-shaped), we acknowledge that many IAS may not have any reported economic costs, let alone costs that conform to a logistic description. IAS impacts are often hard to quantify and monetize (Charles and Dukes 2007), with many economic losses therefore pervasively unreported due to a suite of biases or limited capacity to capture them (Bellard and Jeschke 2016). The cost data selected for this analysis were chosen based on the availability of consistent cost reporting through time by multiple independent sources. While this resulted in the selection of the relatively data-rich genus *Aedes* spp., we highlight that other genera (or species) lacked cost information at a sufficient temporal resolution.

The implications of data limitations are as follows: firstly, given the general tendency to research and record species with higher costs for both management and damage, the cost data available to us through InvaCost are likely skewed to highly damaging species and species requiring costly management. Further, due to lags in IAS detection along with their impacts (Essl et al. 2011), the actual occurrence of impacts is likely earlier on in the timelines, compared to the ones we report in this study, and varies across species and invaded countries (Seebens et al. 2020). Furthermore, our cost saturation estimations could reflect delays in more contemporary cost reporting, and do not preclude the possibility of future spikes in cost due to range expansions of these IAS (Louppe et al. 2019), new types of impacts (e.g., virus emergence) or advances in cost quantification methods, and should therefore be interpreted with caution. Secondly, as our data pooled multiple *Aedes* spp. (although primarily *Aedes aegypti* and *Aedes albopictus*), we did not account for differential environmental tolerances and life histories among congenics

that could influence invasiveness in different regions (Juliano and Lounibos 2005; Medlock et al. 2012, “Appendix A3”). For example, *A. albopictus* is better-adapted to temperate regions due to the production of cold-resistant eggs, with temperate climates reported to preclude *A. aegypti* invasion success (Medlock et al. 2012). Finally, the costs incurred are subject to country-level differences considering, for example, the importance of certain industries (e.g., see estimated impacts to agriculture across different countries in Paini et al. 2016; see map in “Appendix A3”), the different research capacity, effort and funding landscapes, the suitability of habitat for each IAS (Parker et al. 1999), and other socioeconomic or environmental factors that differ across countries.

We note that given the potential for *Aedes* to vector arboviruses at relatively low population densities (Barrera et al. 2019), management of this genus may have been perceived to be necessary by decision makers even at very early invasion stages, which is currently unlikely to be the case for most other IAS. As shown for *Aedes*, one of the most intensively managed IAS with immediate impacts, the investments in management made over the course of more than five decades succeeded in reducing inaction costs in the long-term by 86%. If management had occurred approximately seven years prior, larger savings (\$ 4.57 billion) would have been made for this taxon. It is also worth noting that since InvaCost data are well-known to be prone to underestimation (Diagne et al. 2021), this value is likely a severe underestimation of the true cost savings. The present study estimated the historical trend in *Aedes* management efficiency, however, efficiency can increase or decrease over time due to a range of anthropogenic or biological factors. For *Aedes* and other invaders, our observed increase in efficiency may have been due to changes in policy, increased recognition, technology/skill improvement, or public participation in mitigation strategies (Allen et al., 2021). However, management of other genera or future *Aedes* spp. management may experience the opposite trend due to reduced public participation, biotic facilitation, alternative stable states or phenomena such as emerging resistance to control approaches (e.g., insecticide resistance) (Fung et al. 2011; Moyes et al. 2017; Agha et al. 2021). Future research should address knowledge gaps and focus on further empirical validation, where the suitability of this model is tested across multiple taxa, habitats, and costs from different sectors of the



economy—including situations where management was immediate but could have been costlier if delayed. This calls for more effort into estimating and reporting costs in a standardized way (Diagne et al. 2021).

It is also worth noting that while our analysis was done only on *Aedes* spp, it is likely that in many cases, biosecurity measures and other proactive approaches can be rendered even more cost effective when several species are managed simultaneously. For instance, airport quarantine and interception services deal with very large lists of potential invaders such as insect species, with only marginal costs for each additional species (Lougheed et al. 2007). Aquatic biosecurity measures such as *Check Clean Dry* campaigns and ballast water treatment systems similarly target a range of taxa indiscriminately (e.g., plants, invertebrates, and vertebrates; Anderson et al. 2015; Shannon et al. 2018; Coughlan et al. 2020; Lin et al. 2020). Transport legislation such as wood-packing material treatment protocol ISPM15 can also help minimize IAS risk at that pathway level (Leung et al. 2014; Turbelin et al. 2021). In these cases, modest initial biosecurity investments can yield substantial returns in reduced invasion risk across multiple taxonomic groups.

## Conclusion

There are many well-documented cases where even simple, conceptual models made a direct and significant effect on ecosystem management, in particular assisting in an efficient and cost-saving strategy (e.g., DeAngelis et al. 2021). In studies on biological invasion, mathematical models have been used efficiently for a few decades aiming to identify different invasion scenarios, to reveal the effect of various factors on invasion success and thus to facilitate understanding of the phenomenon (Hengeveld 1989; Shigesada and Kawasaki 1997; Roemer et al. 2002; Courchamp et al. 2004; Lewis et al. 2016). Economic issues such as losses and associated costs have been a focus of modelling studies too (e.g., see Marten and Moore 2011), although this line of research, in our opinion, remains under-developed.

The present study, for the first time, presents a conceptual model which monetizes the cost of inaction surrounding IAS management. While the cost of inaction is often implicitly assumed to be negligible, we show that it can take on a very high value and can

grow quickly from small values at difficult-to-predict threshold times. We hope that this conceptual demonstration can help motivate the collection of necessary cost data that allow for more comprehensive empirical estimates of the cost of inaction. Further, we have confirmed, using our relatively data-rich *Aedes* spp. case study, that more rapid management interventions can greatly reduce inaction costs—at the multi-billion \$ scale over a few decades for this genus alone. Moreover, our cautionary identification of a *runaway* point should motivate timely management prior to the closing of IAS windows of opportunity for efficient and effective control; yet it should also spur immediate management as soon as possible after IAS detection, or ideally, pre-invasion. We expect our results to help resource managers justify early action, even if costly, and accordingly decision makers to fund it, in order to simultaneously increase efficiency and efficacy while decreasing overall costs.

**Author contributions** Conceptualization—DAA, EJH, RNC, MK, PJH, BLR, CL, BL, FC. Dataset (conception, finalisation)—CD, FC, BL. Analyses—DAA, EJH, AB. Methodology—DAA, EJH, BL, FC. Writing—All authors. Visualizations—DAA, PJH, FC.

**Funding** The authors acknowledge the French National Research Agency (ANR-14-CE02-0021) and the BNP-Paribas Foundation Climate Initiative for funding the InvaCost project that allowed the construction of the InvaCost database. The present work was conducted following a workshop funded by the AXA Research Fund Chair of Invasion Biology and is part of the AlienScenarios project funded by BiodivERsA and Belmont-Forum call 2018 on biodiversity scenarios. DAA is funded by the Kuwait Foundation for the Advancement of Sciences (KFAS), grant no. PR1914SM-01 and the Gulf University for Science and Technology (GUST) internal seed fund, grant no. 234597. EJH is supported by a Fonds de recherche du Québec—nature et technologies B3X fellowship. RNC acknowledges funding from the Alexander von Humboldt Foundation. CL was sponsored by the PRIME programme of the German Academic Exchange Service (DAAD) with funds from the German Federal Ministry of Education and Research (BMBF).

**Data availability** The data used in this work come from a publicly available database (InvaCost: <https://doi.org/10.6084/m9.figshare.12668570>). Transformed data used for curve parameterization are provided at <https://github.com/emmajhudsons/CostOfInaction>.

**Code availability** Code and derived data are provided at <https://github.com/emmajhudsons/CostOfInaction>.

## Declarations

**Conflict of interest** The authors have declared that no competing interests exist.

**Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit <http://creativecommons.org/licenses/by/4.0/>.

## Appendix A1: Cost terminology

Vocabulary relating to invasion costs used throughout the manuscript.

Cost type	Definition
Total cost	The sum of <i>management</i> and <i>damage</i> ( <i>cumulative</i> or <i>instantaneous</i> ) costs
Cumulative cost	The sum of ( <i>management</i> , <i>damage</i> , or <i>total</i> ) costs incurred by an IAS since its first reported cost of that type
Marginal cost	The change in the cumulative ( <i>management</i> , <i>damage</i> , or <i>total</i> ) cost of a given IAS between two timesteps (which we model as being equivalent to the <i>instantaneous</i> cost)
Management efficiency	The amount of dollars in reduced damages caused by one dollar spent on management
Cost of inaction	The difference in total cost of an invasion at a given point in time compared to the total cost in a scenario where management began immediately

## Appendix A2: Definitions of parameters and their precise values as used in “Model fitting and results”

The parameter values reported in the manuscript for *Aedes* spp. are rounded for brevity (see “Model fitting and results” and the caption of Fig. 5), whereas

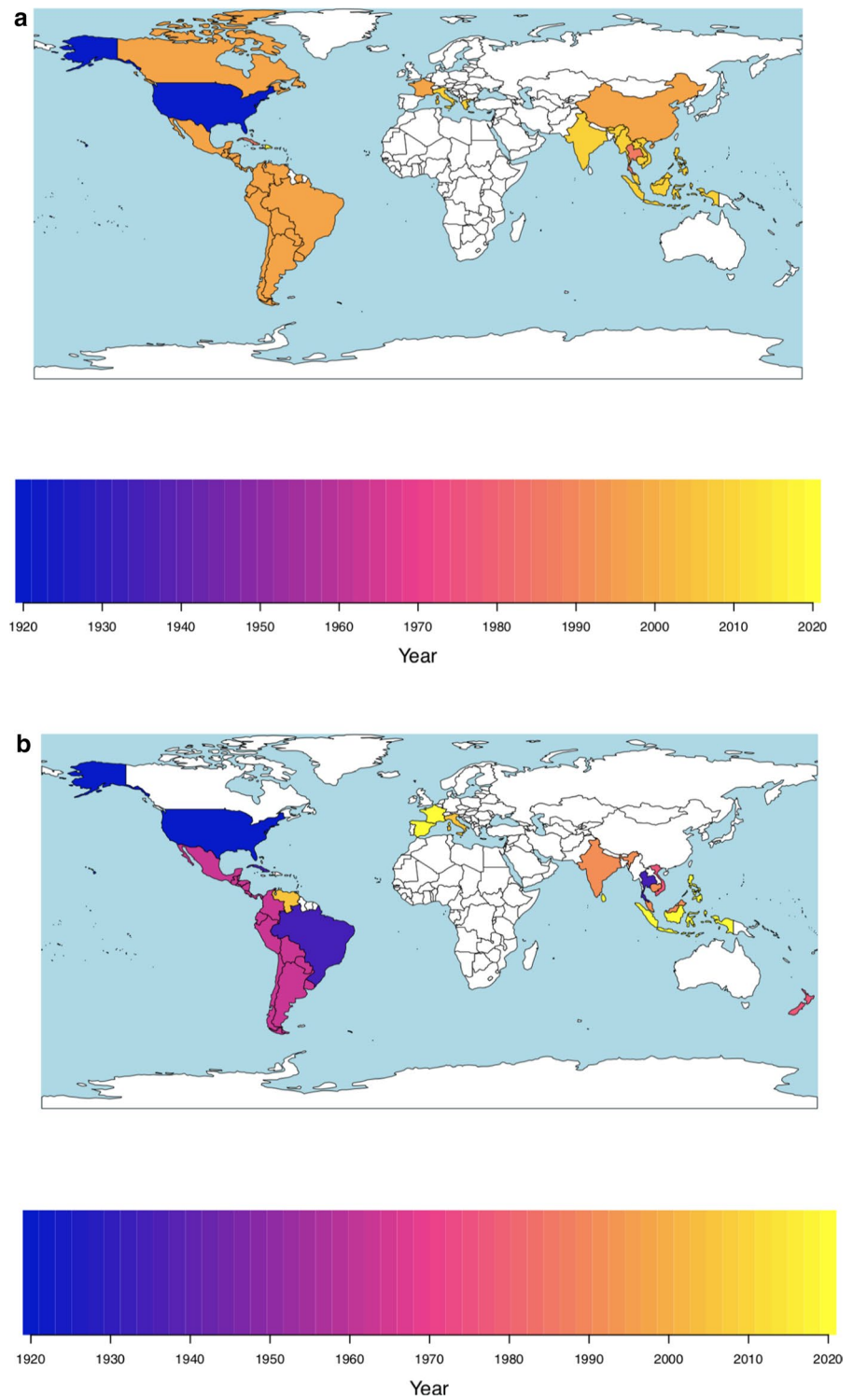
the cost of inaction calculation (see Fig. 6) used estimated best-fit parameters to a higher degree of accuracy. We have also included the definitions of each parameter here for reference.

Management cost parameters			
Intrinsic growth rate for cumulative management costs (year <sup>-1</sup> )	$r_M$	0.290629657870594	
Carrying capacity for cumulative management costs (US\$ millions)	$K_M$	2377.72313470411	
Management cost shape	$A_M$	0.769924032752697	
Initial marginal management cost (US\$ millions)	$M_0$	0.111845162835995	
Damage cost parameters			
Intrinsic growth rate for cumulative damage costs (year <sup>-1</sup> )	$r$	0.33366697569415	
Carrying capacity for cumulative damage costs (US\$ millions)	$K$	99,999.990003501	
Damage cost shape	$A$	0.790808474326249	
Initial marginal damage cost (US\$ millions)	$D_0$	0.263864585318034	
Management efficiency parameters			
Initial management efficiency	$E_0$	1.43984633504595	
Long term management efficiency (for $\alpha > 1$ )	$E_1$	23.0893065550804	
Change in management efficiency (year <sup>-1</sup> )	$\alpha$	0.647071384104067	
Time of management introduction (years) for the observed scenario for <i>Aedes</i> spp.	$\tau$	55 (corresponding to the year 1976)	
Statistical metrics			
Variation explained, management model	$R^2$	0.565681856677696	
Root mean squared error, management model (US\$ millions)	$RMSE$	48.3549208967877	
Variation explained, damage model	$R^2$	0.90651033148684	
Root mean squared error, damage model (US\$ millions)	$RMSE$	453.831424095273	

## Appendix A3: Global map of the first economic impacts over time for *Aedes* spp

See Fig. 7.

**Fig. 7** **a** Damage impacts plotted according to the first record in InvaCost for each country, where applicable. **b** Management impacts plotted according to the first record in InvaCost for each country, where applicable



## References

- Abrahams P, Bateman M, Beale T, Clotley V, Cock M et al (2017) Fall armyworm: impacts and implications for Africa. CABI, Wallingford
- Agha SB, Alvarez M, Becker M, Fèvre EM, Junglen S et al (2021) Invasive alien plants in Africa and the potential emergence of mosquito-borne arboviral diseases—a review and research outlook. *Viruses* 13:32
- Ahmed DA, Hudgins EJ, Cuthbert RN, Haubrock PJ, Renault D et al (2021) Modelling the damage costs of invasive alien species. *Biol Invasions*. <https://doi.org/10.1007/s10530-021-02586-5>
- Allen T, Crouch A, Topp SM (2021) Community participation and empowerment approaches to *Aedes* mosquito management in high-income countries: a scoping review. *Health Promot Int* 36(2):505–523. <https://doi.org/10.1093/heapro/daaa049>
- Anderson LG, Dunn AM, Rosewarne PJ, Stebbing PD (2015) Invaders in hot water: a simple decontamination method to prevent the accidental spread of aquatic invasive non-native species. *Biol Invasions* 17:2287–2297
- Angulo E, Diagne C, Ballesteros-Mejia L, Akulov EN, Dia CAKM et al (2021) Non-English languages enrich scientific data: the example of the costs of biological invasions. *Sci Total Environ* 75:144441
- Barbet-Massin M, Salles J-M, Courchamp F (2020) The economic cost of control of the invasive yellow-legged Asian hornet. *NeoBiota* 55:11–25
- Barrera R, Amador M, Acevedo V, Beltran M, Munoz J (2019) A comparison of mosquito densities, weather and infection rates of *Aedes aegypti* during the first epidemics of Chikungunya (2014) and Zika (2016) in areas with and without vector control in Puerto Rico. *Med Vet Entomol* 33:68–77
- Bellard C, Jeschke JM (2016) A spatial mismatch between invader impacts and research publications: biological invasions and geographic bias. *Conserv Biol* 30:230232
- Bellard C, Rysman J-F, Leroy B, Claud C, Mace GM (2017) A global picture of biological invasion threat on islands. *Nat Ecol Evol* 1:1862–1869
- Charles H, Dukes JS (2007) Impacts of invasive species on ecosystem services. In: Nentwig W (ed) *Biological invasions*. Springer, Berlin, pp 217–237
- Clark CW (1990) *Mathematical bioeconomic. The optimal management of renewable resources*. Wiley, New York
- Coughlan NE, Cuthbert RN, Dick JTA (2020) Aquatic biosecurity remains a damp squib. *Biodivers Conserv* 29:3091–3093
- Courchamp F, Woodroffe R, Roemer G (2004) Removing protected populations to save endangered species. *Science* 302:1532
- Courchamp F, Fournier A, Bellard C, Bertelsmeier C, Bonnaud E et al (2017) Invasion biology: specific problems and possible solutions. *Trends Ecol Evol* 32:13–22
- Crooks JA (2005) Lag times and exotic species: the ecology and management of biological invasions in slow-motion1. *Ecoscience* 12:316–329
- Crystal-Ornelas R, Lockwood JL (2020) The ‘known unknowns’ of invasive species impact measurement. *Biol Invasions* 22:1513–1525
- Cuthbert RN, Diagne C, Hudgins EJ, Turbelin A, Ahmed DA et al (2022) Biological invasion costs reveal insufficient proactive management worldwide. *Sci Total Environ* 819: 52404. <https://doi.org/10.1016/j.scitotenv.2022.153404>
- DeAngelis DL, Franco D, Hastings A, Hilker FM, Lenhart S et al (2021) Towards building a sustainable future: positioning ecological modelling for impact in ecosystems management. *Bull Math Biol* 83:107
- Diagne C, Leroy B, Gozlan RE, Vaissière AC, Assailly C et al (2020a) InvaCost: a public database of the economic costs of biological invasions worldwide. *Sci Data* 7:277
- Diagne C, Catford JA, Essl F, Nuñez MA, Courchamp F (2020b) What are the economic costs of biological invasions? A complex topic requiring international and interdisciplinary expertise. *NeoBiota* 63:25–37
- Diagne C, Leroy B, Vaissière AC, Gozlan RE, Roiz D et al (2021) High and rising economic costs of biological invasions worldwide. *Nature* 592:571–576
- Epanchin-Niell RS (2017) Economics of invasive species policy and management. *Biol Invasions* 19(11):3333–3354. <https://doi.org/10.1007/s10530-017-1406-4>
- Epanchin-Niell RS, Liebhold AM (2015) Benefits of invasion prevention: effect of time lags, spread rates, and damage persistence. *Ecol Econ* 116:146–153
- Essl F, Dullinger S, Rabitsch W, Hulme PE, Hülber K et al (2011) Socioeconomic legacy yields an invasion debt. *Proc Natl Acad Sci USA* 108:203–207
- Finnoff D, Shogren JF, Leung B, Lodge D (2007) Take a risk: preferring prevention over control of biological invaders. *Ecol Econ* 62:216–222
- Francis TB, Abbott KC, Cuddington K, Gellner G, Hastings A et al (2021) Management implications of long transients in ecological systems. *Nat Ecol Evol* 5:285–294
- Fung T, Seymour RM, Johnson CR (2011) Alternative stable states and phase shifts in coral reefs under anthropogenic stress. *Ecology* 92:967–982
- Gardiner SM (2006) A perfect moral storm: climate change, intergenerational ethics and the problem of moral corruption. *Environ Values* 15:397–413
- Hastings A, Hall RJ, Taylor CM (2006) A simple approach to optimal control of invasive species. *Theor Popul Biol* 70(4):431–435. <https://doi.org/10.1016/j.tpb.2006.05.003>
- Haubrock PJ, Bernery C, Cuthbert RN, Liu C, Kourantidou M et al (2021) Knowledge gaps in economic costs of invasive alien fish worldwide. *Sci Total Environ* 803:149875
- Hengeveld R (1989) *Dynamics of biological invasions*. Chapman and Hall, London
- Hoffmann BD, Broadhurst LM (2016) The economic cost of managing invasive species in Australia. *NeoBiota* 31:1–18
- Holmes TP, Aukema JE, Von Holle B, Liebhold A, Sills E (2009) Economic impacts of invasive species in forest past, present, and future. *Ann N Y Acad Sci* 1162:18–38
- Hui C, Richardson DM (2017) *Invasion dynamics*. Oxford University Press, Oxford
- IPBES (2019) Summary for policymakers of the global assessment report on biodiversity and ecosystem services of the intergovernmental science-policy platform on biodiversity and ecosystem services. Bonn, Germany, p 56
- Jones BA (2017) Invasive species impacts on human well-being using the life satisfaction index. *Ecol Econ* 134:250–257

- Jones HP, Holmes ND, Butchart SHM, Tershy BR, Kappes PJ et al (2016) Invasive-mammal eradication on islands results in substantial conservation gains. *Proc Natl Acad Sci USA* 113:4033–4038
- Juliano SA, Lounibos LP (2005) Ecology of invasive mosquitoes: effects on resident species and on human health. *Ecol Lett* 12:435–447
- Kumschick S, Gaertner M, Vilà M, Essl F, Jeschke JM et al (2015) Ecological impacts of alien species: quantification, scope, caveats, and recommendations. *Bioscience* 65:55–63
- Leroy B, Diagne C, Vaissière AC (2020) invacost: INVACOST database with methods to analyse invasion costs. R package version 0.2-4
- Leung B, Lodge DM, Finnoff D, Shogren JF, Lewis MA et al (2002) An ounce of prevention or a pound of cure: bio-economic risk analysis of invasive species. *Proc R Soc B* 269:2407–2413
- Leung B, Springborn MR, Turner JA, Brockerhoff EG (2014) Pathway-level risk analysis: the net present value of an invasive species policy in the US. *Front Ecol Environ* 12:273–279
- Lewis MA, Petrovskii SV, Potts J (2016) The mathematics behind biological invasions. Interdisciplinary applied mathematics. Springer, New York
- Lin Y, Zhan A, Hernandez MR, Paolucci E, MacIsaac HJ, Briski E (2020) Can chlorination of ballast water reduce biological invasions? *J Appl Ecol* 57:331–343
- Lodge DM, Simonin PW, Burgiel SW, Keller RP, Bossenbroek JM et al (2016) Risk analysis and bioeconomics of invasive species to inform policy and management. *Annu Rev Environ Resour* 41:453–488
- Lougheed T (2007) Rooting out invasive species: lessons from down under. *Environ Health Perspect* 115:A352–A357
- Loupe V, Leroy B, Herrel A, Veron G (2019) Current and future climatic regions favourable for a globally introduced wild carnivore, the raccoon *Procyon lotor*. *Sci Rep* 9:1–13
- Marten A, Moore CC (2011) An options based bioeconomic model for biological and chemical control of invasive species. *Ecol Econ* 70:2050–2061
- McDermott SM, Irwin RE, Taylor BW (2013) Using economic instruments to develop effective management of invasive species: insights from a bioeconomic model. *Ecol Appl* 23:1086–1100
- Medlock JM, Hansford KM, Schaffner F, Versteirt V, Hendrickx G et al (2012) A review of the invasive mosquitoes in Europe: ecology, public health risks, and control options. *Vector Borne Zoonotic Dis* 12:435–447
- Moyes CL, Vontas J, Martins AJ, Ng LC, Koou SY et al (2017) Contemporary status of insecticide resistance in the major *Aedes* vectors of arboviruses infecting humans. *PLoS Negl Trop Dis* 15:e0009084
- Paini DR, Sheppard AW, Cook DC, De Barro PJ, Worner SP et al (2016) Global threat to agriculture from invasive species. *Proc Natl Acad Sci USA* 113:7575–7579
- Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M et al (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biol Invasions* 1:3–19
- Pejchar L, Mooney HA (2009) Invasive species, ecosystem services and human well-being. *Trends Ecol Evol* 24:497–504
- Polasky S (2010) A model of prevention, detection, and control for invasive species. In: Perrings C, Mooney H, Williamson M (eds) *Globalization and bioinvasions: ecology, economics, management and policy*. Oxford University Press, Oxford, pp 100–109
- Pyšek P, Richardson DM, Pergl J, Jarošík V, Sixtová Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. *Trends Ecol Evol* 23:237–244
- Pyšek P, Hulme PE, Simberloff D, Bacher S, Blackburn TM et al (2020) Scientists' warning on invasive alien species. *Biol Rev* 95:1511–1534
- Ricciardi A, MacIsaac HJ (2011) Impacts of biological invasions on freshwater ecosystems. *Fifty Years Invasion Ecol* 1:211–224
- Roemer G, Donlan J, Courchamp F (2002) Golden eagles, feral pigs and insular carnivores: how exotic species turn native predators into prey. *Proc Natl Acad Sci USA* 99:791–796
- Russell JC, Innes JG, Brown PH, Byrom AE (2015) Predator-free New Zealand: conservation country. *Bioscience* 65:520–525
- Schaffner U, Steinbach S, Sun Y, Skjøth CA, de Weger LA et al (2020) Biological weed control to relieve millions from *Ambrosia* allergies in Europe. *Nat Commun* 11:1745
- Seebens H, Blackburn TM, Dyer EE, Genovesi P, Hulme PE et al (2017) No saturation in the accumulation of alien species worldwide. *Nat Commun* 8:14435
- Seebens H, Clarke DA, Groom Q, García-Berthou E, Kühn I et al (2020) A workflow for standardising and integrating alien species distribution data. *NeoBiota* 59:39–59
- Shabani F, Ahmadi M, Kumar L, Sohljouy-Fard S, Tehrani MS et al (2020) Invasive weed species' threats to global biodiversity: future scenarios of changes in the number of invasive species in a changing climate. *Ecol Indic* 116:106436
- Shannon C, Quinn CH, Stebbing PD, Hassall C, Dunn AM (2018) The practical application of hot water to reduce the introduction and spread of aquatic invasive alien species. *Manage Biol Invasions* 9:417–423
- Shepard DS, Coudeville L, Halasa YA, Zambrano B, Dayan GH (2011) Economic impact of dengue illness in the Americas. *Am J Trop Med Hyg* 84:200–207
- Shigesada N, Kawasaki K, Takeda Y (1995) Modeling stratified diffusion in biological invasions. *Am Nat* 146(2):229–251. <https://doi.org/10.1086/285796>
- Shigesada N, Kawasaki K (1997) *Biological invasions: theory and practice*. Oxford University Press, Oxford
- Simberloff D, Marti J-L, Genovesi P, Maris V, Wardle DA et al (2013) Impacts of biological invasions: what's what and the way forward. *Trends Ecol Evol* 28:58–66
- Sims C, Finnoff D, Shogren JF (2016) Bioeconomics of invasive species: using real options theory to integrate ecology, economics, and risk management. *Food Secur* 8:61–70
- Timmins SM, Braithwaite H (2002) Early detection of invasive weeds on islands. In: Veitch CR, Clout MN (eds) *Turning the tide: the eradication of invasive species*. IUCN, Gland, pp 311–318
- Turbelin AJ, Diagne C, Hudgins EJ, Moodley D, Haubrock PJ et al (2021) Species on the move: stowaways and



contaminants cause the greatest economic impacts. ResearchSquare, pre-print. <https://doi.org/10.21203/rs.3.rs-440305/v1>

Victorian Government (2010) Invasive plants and animals policy framework. DPI Victoria, Melbourne

Vilà M, Basnou C, Pyšek P, Josefsson M, Genovesi P et al (2010) How well do we understand the impacts of alien

species on ecosystem services? A pan-European, cross-taxa assessment. *Front Ecol Environ* 8:135–144

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.